

Species richness and abundance of ectomycorrhizal basidiomycete sporocarps on a moisture gradient in the *Tsuga heterophylla* zone

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Abstract: Sporocarps of epigeous ectomycorrhizal fungi and vegetation data were collected from eight *Tsuga heterophylla* (Raf.) Sarg. – *Pseudotsuga menziesii* (Mirb.) Franco stands along a wet to dry gradient in Olympic National Park, Washington, U.S.A. One hundred and fifty species of ectomycorrhizal fungi were collected from a total sample area of 2.08 ha. Over 2 years, fungal species richness ranged from 19 to 67 taxa per stand. Sporocarp standing crop ranged from 0 to 3.8 kg/ha, averaging 0.58 kg/ha, 0.06 kg/ha in spring and 0.97 kg/ha in fall. Sporocarp standing crop and fungal species richness were correlated with precipitation. These results demonstrated that ectomycorrhizal fungal sporocarp abundance and species richness can be partly explained in terms of an environmental gradient.

Key words: fungi, old growth, species richness, sporocarp production, detrended correspondence analysis.

Résumé : Les auteurs ont récolté les sporocarpes de champignons ectomycorhiziens épigés ainsi que des données sur la végétation, à partir de huit peuplements de *Tsuga heterophylla* (Raf.) Sarg. – *Pseudotsuga menziesii* (Mirb.) Franco, le long d'un gradient passant de l'humide au sec, dans le parc national Olympic, de l'état de Washington. A partir d'une surface totale d'échantillonnage de 2,08 ha, ils ont obtenu 150 espèces de champignons ectomycorhiziens. Au cours des deux années d'observation, la richesse fongique en espèces va de 19 à 67 taxons par peuplement. La biomasse des sporocarpes sur pied va de 0 à 3,8 kg/ha, avec une moyenne de 0,58 kg/ha, soit 0,06 kg/ha au printemps et 0,97 kg/ha à l'automne. Il existe une corrélation entre la biomasse fongique sur pied et la richesse floristique, avec les précipitations. Ces résultats démontrent que l'abondance et la richesse en espèces des champignons ectomycorhiziens peut s'expliquer en partie en terme d'un gradient environnemental.

Mots clés : champignons, vieille forêt, richesse en espèces, production de sporocarpes, analyse par correspondance, hors tendances.

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Introduction

Ectomycorrhizal fungi (EMF) often are considered an ecological guild distinguished by their stable biotrophic association with the roots of woody plants and production of macroscopic sporocarps (Bills et al. 1986; Luoma et al. 1991). Ectomycorrhizae are formed when fungi colonize the roots of woody plants. Colonization of roots by the fungi, the normal condition, stimulates root production and increases the availability of nutrients and water to the host (Smith and Read 1997). Worldwide, an estimated 5400 species of fungi form ectomycorrhizal associations with most dominant woody plant families (e.g., Betulaceae, Fagaceae, Pinaceae, Myrtaceae; Molina et al. 1992).

Ectomycorrhizal fungi profoundly affect the host plants increasing their survival, growth, and competitive ability (Perry et al. 1989). The fungi benefit by receiving 30–60% of the net photosynthate produced by the host (Norton et al. 1990; Simard et al. 1997a). Fungal mycelia also provide an avenue for translocation of significant amounts of carbon among hosts of the same and different species (Simard et al. 1997a, 1997b). It is likely that carbon translocation benefits understory seedlings during establishment and may affect interspecific and intraspecific competition (Perry et al. 1992).

Ectomycorrhizal fungi provide a major link between carbon fixed by primary producers and other trophic levels in the ecosystem. For example, several rodent species rely on EMF sporocarps for 90% of their diet (Maser et al. 1978;

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Hayes et al. 1986). Ungulates, bacteria, arthropods, and other species of fungi also use or depend on EMF sporocarps as a source of food and perhaps micronutrients.

Despite the importance of ectomycorrhizal fungi to ecosystem structure and function, field ecological studies of these organisms have been relatively limited (Klironomos and Kendrick 1993). Much of the research to date has been devoted to documenting differences in EMF species composition among forests with different host tree species. Many EMF species are host generalists, but others colonize the roots of particular genera or families of woody plants (Molina and Trappe 1982; Massicotte et al. 1994). Differences in EMF communities are particularly evident when forest communities dominated by hardwoods are compared with those dominated by conifers (Bills et al. 1986; Villeneuve et al. 1989; Nantel and Neuman 1992). The distribution of EMF species, then, is partly driven by the presence of their associated host species.

Environmental gradients, particularly precipitation, often help explain patterns of species or community distribution across landscapes (e.g., Whittaker and Niering 1975; Zobel et al. 1976; Barbour et al. 1987; Rosenzweig and Abramsky 1993). The distribution of EMF species is also potentially affected by moisture availability. Luoma (1989) and Luoma et al. (1991) suggest that a combination of precipitation and stand age influenced the distribution of hypogeous (fruiting below ground) EMF in forests of the central Oregon Cascade Range; however, few studies have attempted to relate EMF distribution to environmental gradients independent of host. Indeed, even though moisture availability is known to be a crucial factor in the fruiting of fungi (Eveling et al. 1990), precipitation was largely ignored as an important factor affecting species distributions in a recent review of fungal community ecology (Winterhoff 1992).

Most published studies of macrofungal communities in the Pacific Northwest since Cooke (1955) have focused on hypogeous fungi (e.g., Fogel and Hunt 1979; Hunt and Trappe 1987; Luoma et al. 1991; North et al. 1997). Hypogeous fungi are an ecologically important part of the EMF group, but they account for only about 20% of all species of EMF (Molina et al. 1992). The remaining 80% of EMF are epigeous (fruiting above ground) and remain less studied.

Recently, declines in EMF richness in Europe have led to many species being listed as rare or threatened (Arnolds 1988; Arnolds and DeVries 1993). In the Pacific Northwest United States, Federal land management agencies are now required to survey or manage for 225 species of fungi, about half of which are ectomycorrhizal (USDA and USDI 1994a, 1994b). Because concern is growing over the effects of forest management practices on the fate of fungi, data are needed on fungal species and environmental relations to aid in sound ecosystem management (O'Dell et al. 1996).

Our study was designed to examine changes in sporocarp occurrence and abundance of EMF species along an environmental gradient where host tree species are constant. The Olympic Peninsula, Washington, with large areas of old-growth coniferous forests in Olympic National Park, is an ideal place to study relations of species to the environment. The topography and steep precipitation and elevational gradients produce sites with dissimilar climates in close prox-

imity. Here, we present data on epigeous EMF and vascular plant community attributes in eight old-growth coniferous forest stands in Olympic National Park. Stands spanned a wet to dry gradient in the *Tsuga heterophylla* (Raf.) Sarg. zone (sensu Franklin and Dyrness 1988). Plant associations, EMF sporocarp species richness, sporocarp standing crop, and community structure are related to the precipitation gradient.

Methods

Study area

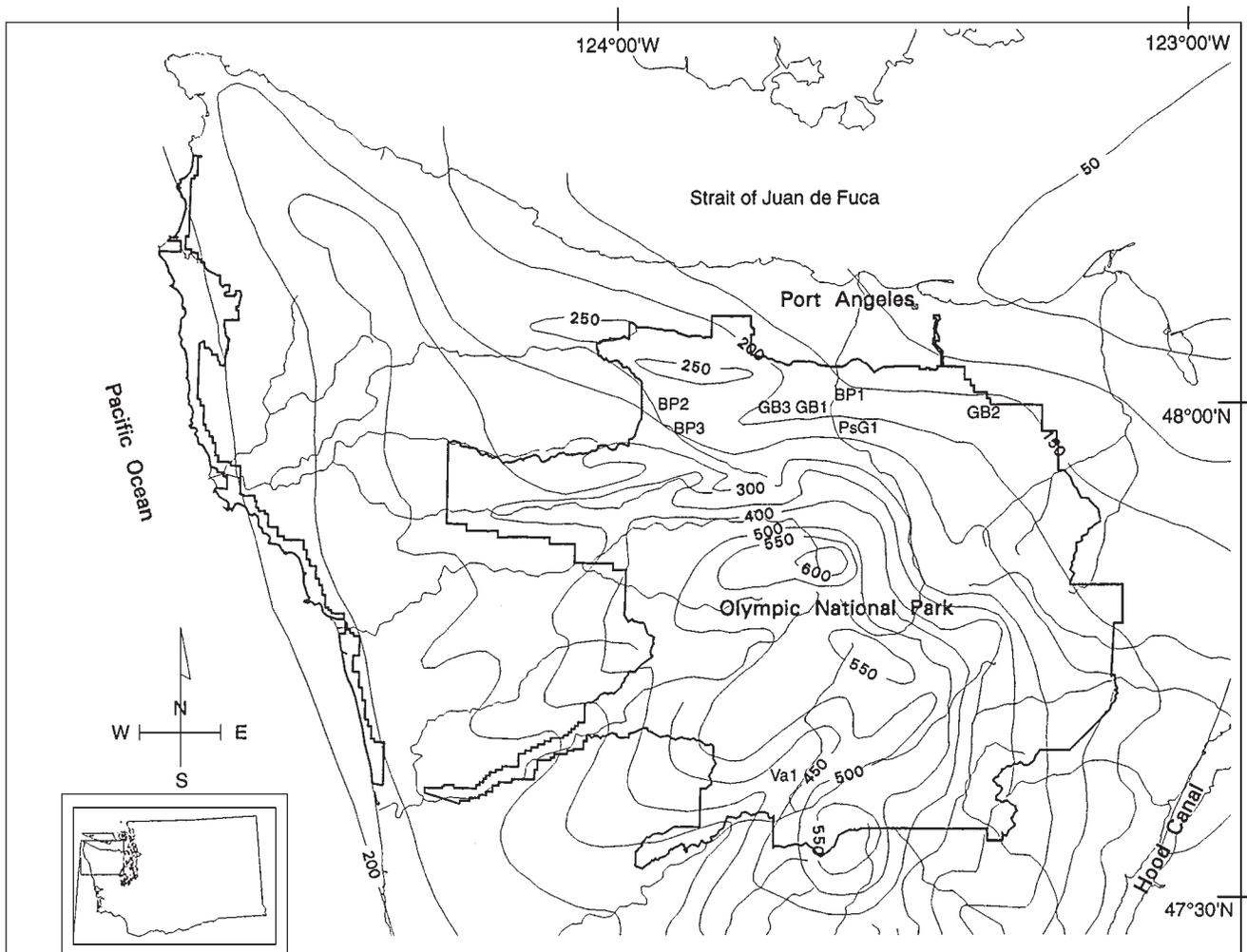
The 13 800 km² Olympic Peninsula is located in the northwestern corner of the conterminous United States from lat. 46°30' to 48°25'N and long. 122°40' to 124°45'W. The peninsula is bounded on the west by the Pacific Ocean, on the north by the Strait of Juan de Fuca, and on the east by Hood Canal, a fjordlike extension of Puget Sound (Fig. 1). We consider the southern boundary of the peninsula to extend from the tip of Hood Canal to the Chehalis River and west to Grays Harbor. The Olympic Mountains rise sharply from the surrounding coastal plain and foothills. Mount Olympus is the highest peak at 2430 m; 37 other major peaks exceed 2130 m. Eleven major rivers radiate from the mountainous core.

The Olympic Mountains block the flow of moist air from the Pacific Ocean, producing heavy precipitation on the west side of the peninsula and a striking rain shadow on the northeast flanks (Fig. 1). Mount Olympus receives more than 600 cm of precipitation annually, whereas the community of Sequim, only 55 km distant, receives just 45 cm (Phillips and Donaldson 1972). Eighty percent of the peninsula's annual precipitation falls between October and March with only 5% occurring in July and August (Phillips and Donaldson 1972; National Oceanic and Atmospheric Administration 1978). Winter precipitation falls mostly as rain below 300 m elevation. At low elevations, average January temperatures are near 0°C, and average maximum August temperatures are about 21°C.

Low-elevation forests of the Olympic National Park occur mainly in the *Tsuga heterophylla* and *Picea sitchensis* zones (Franklin and Dyrness 1988). The *Tsuga heterophylla* zone, often dominated by enormous *Pseudotsuga menziesii* (Mirb.) Franco with *Thuja plicata* and *Tsuga heterophylla*, is the most common forest zone in the park (Buckingham et al. 1995). Lowland forests in valleys of the western portion of the Park lie mainly within the *Picea sitchensis* zone. The famous rain forests of the west-side river valleys are distinguished by massive *Picea sitchensis* up to 90 m tall and *Acer macrophyllum* laden with epiphytic mosses, clubmosses, and ferns.

We selected eight stands (Fig. 1) dominated by large old-growth *Pseudotsuga menziesii* and *Tsuga heterophylla* across a precipitation gradient in Olympic National Park. We chose stands with lateral conditions to avoid differences resulting from disturbance and succession, and stands representative of dominant plant associations of the region that represent a moisture gradient. All stands were in the *Tsuga heterophylla* zone, although one stand was about 50 m from stands falling into the *Picea sitchensis* zone on an adjacent, lower, river terrace. Stand selection criteria included low abundance of other mycorrhizal host tree species, such as *Abies* spp. (true fir) and *Alnus rubra* (red alder); structural characteristics of old-growth forests, such as a multilayered canopy, large individuals of secondary successional species (i.e., *Tsuga heterophylla*), large snags and considerable quantities of downed large organic woody debris; and lack of any obvious human disturbance.

Fig. 1. The Olympic Peninsula, with stand locations and average annual precipitation isoclines (cm).



Vascular plants and stand characteristics

Two 500- or 1000-m² circular plots, large enough to include at least 40 trees and saplings, were established to measure forest community characteristics at each stand. Plots were located to represent typical vegetation in the study area. We measured diameter at breast height (dbh) of all trees over 1 cm dbh and slope and aspect of the plot. We also estimated percentage of cover of each species of vascular plants, and combined percentage of cover of all species of mosses and lichens in classes of <1, 1–5, 6–25, 26–50, 51–75, 76–95, and 96–100% and cover of large woody debris in each of five decay classes following Maser and Trappe (1984). To estimate stand age, we took increment cores from two to five trees in each major size class. The rings in these cores were counted by using a video camera attached to a dissecting microscope and video monitor. We cored dominant *Pseudotsuga menziesii* in or adjacent to each plot until we obtained at least two cores from separate individuals that reached the pith. The *Pseudotsuga menziesii* inside plots occasionally had heart rot or were too large to core, which necessitated the use of trees adjacent to the plot. Vascular plant nomenclature follows Hitchcock and Cronquist (1976) as updated by Buckingham et al. (1995).

Mean annual precipitation at each study site was estimated using a digitized version of the map in Phillips and Donaldson (1972, see Fig. 1). Isolines of mean annual precipitation were first plotted

on a topographic map of the Olympic Peninsula, and then the GIS program ARC/INFO™ was used to estimate precipitation at each study site.

Sporocarp sampling

Epigeous fungal sporocarps were sampled two or three times each fall and spring from September 1992 to June 1994. Two transects, each containing fifty 4-m² circular plots at 5-m intervals, were sampled in each stand on each sample date (400-m² sample area). The second transect was placed parallel and 5 m away from the first; two new transects were established each sample period. This method was intended to minimize the potential effects of removing sporocarps from plots, by changing their location for each sample, and to efficiently sample spatially patchy sporocarps, by dispersing plots. A total of 2.08 ha (~0.26 ha per stand) in 104 transects was sampled over 2 years. Sporocarps of ectomycorrhizal genera (following Miller 1983 and Molina et al. 1992) were collected from each plot, identified, dried at about 60°C for at least 48 h, and weighed to obtain dry weight. Field identifications were confirmed by microscopic examination. Over 160 taxa of EMF were detected in sample plots; 150 taxa could be identified to species. Some collections were unidentifiable owing to lack of taxonomic resources for North America, inadequate documentation of fresh characters, or decrepitude of specimens.

Table 1. Location, plant association, and environmental characteristics of eight forest stands in Olympic National Park included in the study.

	Deer Creek	Deer Park Rd.	Hell Creek	Whiskey Bend	Elwha Campground Trail	N. Fork Soleduc River Trail	Soleduc Falls Trail	Irely Lake Trail
Stand Code	Ga1	Ga2	Ga3	PsG1	BP1	BP2	BP3	Va1
Plant association	<i>Tsuga heterophylla</i> – <i>Gaultheria shallon</i>	<i>Tsuga heterophylla</i> – <i>Gaultheria shallon</i>	<i>Tsuga heterophylla</i> – <i>Gaultheria shallon</i>	<i>Pseudotsuga menziesii</i> – <i>Gaultheria shallon</i>	<i>Tsuga heterophylla</i> – <i>Berberis nervosa</i> – <i>Polystichum munitum</i>	<i>Tsuga heterophylla</i> – <i>Berberis nervosa</i> – <i>Polystichum munitum</i>	<i>Tsuga heterophylla</i> – <i>Berberis nervosa</i> – <i>Polystichum munitum</i>	<i>Tsuga heterophylla</i> – <i>Vaccinium alaskense</i>
Mean annual precipitation (cm)	202	163	203	243	154	231	251	457
Elevation (m)	403	770	658	421	124	545	692	175
% slope	6	17	27	27	7	26	18	3
Aspect	S64W	S18E	S28E	S30W	N37W	N81W	S27W	N70E
Maximum tree age (years)	309	294	304	297	311	247	271	246
Maximum dbh (cm)	79	50	112	114	145	104	124	162
Total basal area (m ² /ha)	72	69	114	63	89	77	96	67
Basal area of ectomycorrhizal host species	69	66	106	62	90	78	96	67
Total shrub cover	77	80	77	91	24	38	48	51

Table 2. Average percent cover by stratum of vascular plants and ferns in two 500- or 1000-m² plots at eight stands in Olympic National Park.

Stratum and species	Ga1	Ga2	Ga3	PsG1	BP1	BP2	BP3	Va1
Canopy								
<i>Pseudotsuga menziesii</i> *	52.5	45	55	100	35	47.5	70	20
<i>Thuja plicata</i>	5	0.3	4.5					
<i>Tsuga heterophylla</i>	47.5	55	40		65	52.5	30	90
Sapling								
<i>Acer circinatum</i>			0.5			0.5		
<i>Tsuga heterophylla</i>	1.75	0.5	8	1.55		1.55	15.5	
Seedling								
<i>Acer circinatum</i>	0.5					0.1		
<i>Tsuga heterophylla</i>	0.5		0.3	0.1	0.1	0.1	3	1.75
<i>Pseudotsuga menziesii</i>				0.1				0.1
Understory								
<i>Achlys triphylla</i>			0.1	0.3	0.5		0.1	
<i>Berberis nervosa</i>	1.75	1.75	1.75	44.25	1.55	0.5	9.25	
<i>Chimaphila menziesia</i>			3	0.3	0.1	0.5	0.1	
<i>Chimaphila umbellata</i>		0.5	3	0.1				
<i>Clintonia uniflora</i>							3	3
<i>Coralarhiza</i> spp.	0.5				1.55	0.1		
<i>Cornus unalaskense</i>			0.5				0.5	3
<i>Galium</i> sp.				0.1			0.1	
<i>Gaultheria shallon</i> †	61.75	74.25	38	44.25		0.1	0.3	
<i>Goodyeara oblongifolia</i>	0.5			0.1	0.1	0.1		
<i>Linnea borealis</i>		0.5	1.75	3	0.1	0.5	0.3	
<i>Listera cordata</i>	0.1	0.1	0.3	0.1		0.5	0.5	
<i>Menziesia ferruginea</i>							0.5	0.1
<i>Monotropa hypopitys</i>	0.1				0.1			
<i>Polystichum munitum</i>			0.5	0.1	9.25	1.75	1.75	0.1
<i>Pteridium aquifolium</i>				0.1		0.1		3
<i>Rosa gymnocarpa</i>			0.3	0.5				
<i>Rubus ursinus</i>	0.1		0.1					
<i>Tiarella trifoliata</i>			0.3				0.5	0.5
<i>Trientalis latifolium</i>				0.1	0.1			
<i>Trillium ovatum</i>		0.1		0.1	0.1	0.1	0.1	
<i>Vaccinium alaskense</i>			0.1				3	26.75
<i>Vaccinium parvifolium</i>	1.55	0.1	1.75	0.1	0.1	0.5	0.5	0.5
<i>Viola sempervirens</i>			0.1	0.5	0.1			

*Ectomycorrhizal host genera are listed in bold.

†*Gaultheria shallon* apparently forms ectomycorrhizae on a small percentage of roots; the significance of this for fungal species occurrence (e.g., existence of *Gaultheria*-specific ectomycorrhizal fungi) is not known.

Data analyses

Sporocarp and vascular plant data were summarized by stand. Percentage of cover of each vascular plant species was averaged for the two plots at each stand. Sporocarp biomass values were converted to total standing crop in grams per hectare. Plant associations were determined from keys in Henderson et al. (1989).

Plant cover and EMF standing crop were analyzed separately by using detrended correspondence analysis (DCA) following Hill and Gauch (1980) in the software package PCORD (McCune and Mefford 1995). We used relative plant cover for each stratum (i.e., trees, shrubs, and herbs and ferns) and relative sporocarp standing crop as inputs to DCA. Species occurring in a single stand were omitted. The following default DCA options were used: down-weighting rare species, rescaling axes, cutoff residual of 0.0001, and 26 segments.

Linear regressions were calculated in STATVIEW 4.0 software (Abacus Concepts 1992) by using the DCA axis 1 from each or-

dination, sporocarp standing crop, and EMF species richness as dependent variables and stand characteristics and precipitation as independent variables. For regressions on precipitation, one stand (Va1, Table 1) was omitted as an outlier. This stand had over twice as much average annual precipitation as the next wettest stand, leaving a large gap in the precipitation gradient.

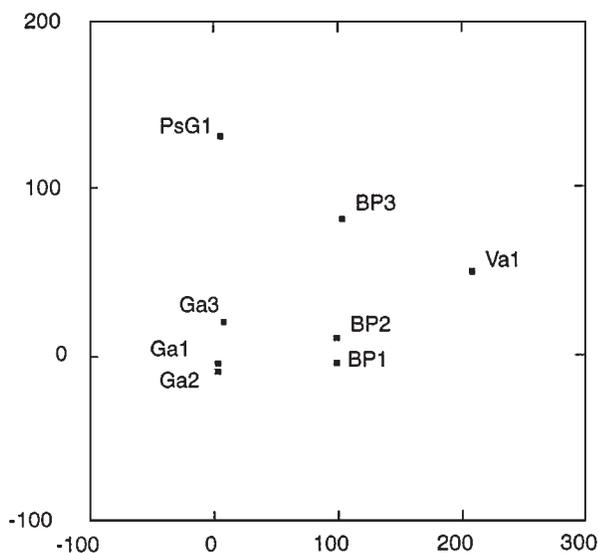
Results

Stand and vegetation characteristics

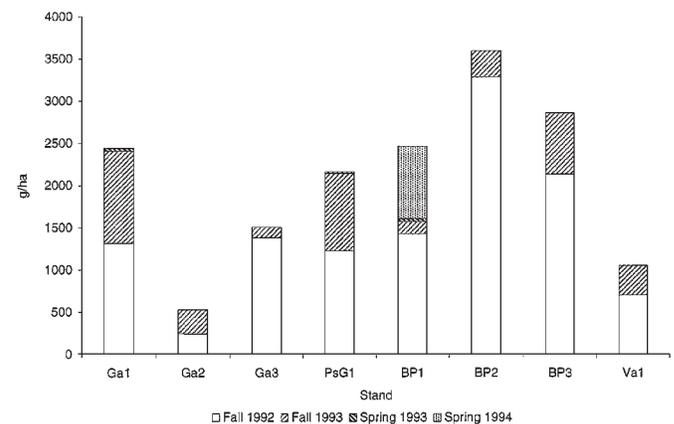
Stands were dominated by *Tsuga heterophylla* and *Pseudotsuga menziesii*, which accounted for 95–100% of canopy cover (Table 2). Other ectomycorrhizal plant species present in low abundance (less than 1% cover) were *Abies amabilis*, *Abies grandis*, *Alnus rubra*, *Arbutus menziesii*, *Arctostaphylos uva-ursi*, *Picea sitchensis*, and *Pinus monti-*

Table 3. R^2 values for regressions of environmental variables, vegetation, and EMF attributes from eight stands in Olympic National Park.

Environmental variable	Vegetation DCA1	Fungi DCA1	Sporocarp standing crop	EMF richness
Precipitation	0.0	0.51*	0.51*	0.67 [†]
Elevation	0.37	0.27	0.01	0.09
% slope	0.28	0.06	0.05	0.21
Age	0.42*	0.35	0.04	0.03
Maximum dbh	0.61 [†]	0.66 [†]	0.0	0.0
Basal area	n.d.	0.0	0.03	0.08
Basal area ectomycorrhizal hosts	n.d.	0.0	0.06	0.1
Basal area <i>Pseudotsuga menziesii</i>	n.d.	0.02	0.0	0.01
Total shrub cover	n.d.	0.23	0.27	0.19
<i>Gaultheria shallon</i> cover	n.d.	0.42*	0.13	0.06
<i>Vaccinium</i> spp. cover	n.d.	0.57 [†]	0.11	0.16
<i>Tsuga heterophylla</i> cover	n.d.	0.08	0.13	0.23
<i>Pseudotsuga menziesii</i> cover	n.d.	0.04	0.13	0.21
Total large woody debris cover	n.d.	0.02	0.0	0.0
Class IV large woody debris cover	n.d.	0.55 [†]	0.12	0.09
Class V large woody debris cover	n.d.	0.24	0.21	0.32

* $p < 0.10$.[†] $p < 0.05$.**Fig. 2.** Plant species DCA stand scores on axes 1 and 2, with eigenvalues of 0.43 and 0.14, respectively.

cola. All stands included some trees over 240 years old (maximum 311). In some stands, however, much of the canopy was dominated by younger age classes. Standing volume was variable among stands; maximum dbh ranged from 50.9 to 162.5 cm, and total basal area of woody stems ranged from 63 to 114 m²/ha (Table 1). Stands fell into three plant associations within the *Tsuga heterophylla* zone and one in the *Pseudotsuga menziesii* zone from the keys in Henderson et al. (1989). Three stands fit the *Tsuga heterophylla* – *Berberis nervosa* – *Polystichum munitum* association (BP1, BP2, BP3), three fit the *Tsuga heterophylla* – *Gaultheria shallon* association (Ga1, Ga2, Ga3), one fit the *Tsuga heterophylla* – *Vaccinium alaskense* association (Va1), and one fit the *Pseudotsuga menziesii* – *Gaultheria shallon* association (PsG1).

Fig. 3. Annual variation in EMF sporocarp standing crop (g/ha) by stand and season.

Twenty-seven plant species occurred at two or more stands and were included in the ordination (Table 2). The first DCA axis had an eigenvalue of 0.34 and a length of 2.09 standard deviations (Fig. 2). The plant associations are clearly segregated along DCA axis 1. The four plant associations are clearly segregated in a plot of the ordination (Fig. 2), but it is not clear if environmental variables are closely linked with either DCA axis. Axis 1 may be linked with precipitation, but this was not evident in the linear regression analyses (Table 3). The R^2 between estimated precipitation and DCA axis 1 was 0.0.

Sporocarp productivity and richness

The total sporocarp biomass collected was 1.53 kg. Sporocarp standing crop ranged from 0.00 to 3.80 kg/ha per stand sample, mean was 0.58 kg/ha, 0.06 kg/ha in spring, and 0.97 kg/ha in fall (Fig. 3). Fall sporocarp standing crop for each species by stand is given in Table 4. The maximum for a single species, averaged across all stands, was 0.11 kg/ha for *Hydnum repandum*, followed by *Lactarius pseudomuci-*

Table 4. Total fall standing crop of ectomycorrhizal sporocarps from eight stands in Olympic National Park, 1992 and 1993.

	Ga1	Ga2	Ga3	PsG1	BP1	BP2	BP3	Va1
<i>Amanita constricta sensu lato</i>						6.1		10.2
<i>Amanita franchetii</i>							6.8	
<i>Amanita pachycolea</i>					93			8.2
<i>Amanita porphyria</i>				3.2				
<i>Amanita silvicola</i>					25			
<i>Boletus mirabilis</i>							47	1.4
<i>Boletus zelleri</i>			36			5.1		188
<i>Cantharellus formosus</i>			22			126	38	28
<i>Cantharellus subalbidus</i>						74		
<i>Cantharellus tubaeformis</i>	23		46			58	158	
<i>Chroogomphus tomentosus</i>	54	4.1	8.8		96	14	25	
<i>Cortinarius acutus</i> gp.			2.8			0.6		
<i>Cortinarius agathosmus</i> gp.							15	
<i>Cortinarius aimatochelis sensu Moser</i>	4.9					6.3		
<i>Cortinarius alboviolaceus</i>	10					8.5		
<i>Cortinarius badiovinaceus</i>		1.4					49	
<i>Cortinarius bicolor complex</i>						12		
<i>Cortinarius boulderensis</i>	12				0.2			
<i>Cortinarius brunneus</i>	165	18	21			27		
<i>Cortinarius cacaoacolor</i>							8.1	
<i>Cortinarius clandestinus</i>	3.3	2.9	12			22		
<i>Cortinarius claricolor</i> gp.	68			27	14			
<i>Cortinarius compar</i> gp.	3.3	7.6						
<i>Cortinarius comptulus</i> gp.	18	5.3			104			
<i>Cortinarius depauperatus</i>			3				1	
<i>Cortinarius dilutus</i> gp.							4.1	
<i>Cortinarius evernius</i> gp.						6	7.3	
<i>Cortinarius gentilis</i>	9.1	4.5				11		
<i>Cortinarius griseoviolaceus</i>			15				20	
<i>Cortinarius infractus</i>				17				
<i>Cortinarius junghunii</i> gp.			1.5	0.9		7.4		
<i>Cortinarius laetus</i> gp.				1.5				
<i>Cortinarius laniger</i> gp.	9.4			33				
<i>Cortinarius latus</i> gp.	14	12	105	8.9	29			
<i>Cortinarius lebretonii</i>	28		19					
<i>Cortinarius malachius complex</i>						29		
<i>Cortinarius montanus</i>				11			62	
<i>Cortinarius muscigenus</i>	23							
<i>Cortinarius mutabilis</i>	3.8				99	23		
<i>Cortinarius obtusus</i> gp.	4.3		13				8.9	
<i>Cortinarius olympianus</i>		55			2.1			
<i>Cortinarius orichalceus complex</i>			14					
<i>Cortinarius paleaceus</i> gp.	2.2			0.4				
<i>Cortinarius papulosus</i>	6.3						17	
<i>Cortinarius paragaudis</i> gp.		7.5	3.1				5	
<i>Cortinarius pseudocolus</i> gp.					6.5			
<i>Cortinarius rapaceus</i> gp.				6.9	18	2.6	17	
<i>Cortinarius renidens</i>				8.4		7.6		
<i>Cortinarius rubicundulus complex</i>			3.5					
<i>Cortinarius salor</i> gp.	14							
<i>Cortinarius sebaceus</i>							5.8	
<i>Cortinarius</i> sp., section <i>pulchelli</i>	1.8							
<i>Cortinarius</i> sp. <i>Leprocybe</i>						1.8		
<i>Cortinarius</i> sp. <i>Myxacium</i> 1	2						9.3	
<i>Cortinarius</i> sp. <i>Telemonia</i> 10							23	
<i>Cortinarius</i> sp. <i>Telemonia</i> 8							139	
<i>Cortinarius</i> sp. <i>Telemonia</i> 9							12	

Table 4. (continued).

	Ga1	Ga2	Ga3	PsG1	BP1	BP2	BP3	Va1
<i>Cortinarius stemmatus</i> gp.	0.2							
<i>Cortinarius stillatitus</i> gp.							5.4	
<i>Cortinarius strobilaceus</i>							24	
<i>Cortinarius superbus</i>				211				
<i>Cortinarius tabularis</i> gp.		46					15	
<i>Cortinarius traganus</i>	34						37	
<i>Cortinarius vanduzerensis</i>						8.8	7.3	
<i>Cortinarius vibratilis</i> gp.	11	2.9	1.2		9.9		6.9	
<i>Cortinarius zinziberatus</i>		1.5	3.3					
<i>Cortinarius</i> aff. <i>zinziberatus</i> 1	16	3.7	1.5	16				
<i>Cortinarius</i> aff. <i>zinziberatus</i> 2							2.9	
<i>Dermocybe crocea</i> gp.						0.9		1.1
<i>Dermocybe idahoensis</i>			21	3.3		8	3	
<i>Dermocybe malicoria</i>						63	38	
<i>Dermocybe neskowinensis</i> gp.			1.4					
<i>Dermocybe phoenicea</i> v. <i>occidentalis</i>	5.6							
<i>Dermocybe sanguinea</i>							2.6	
<i>Dermocybe semisanguinea</i>	15	4.1	28			13	1.1	
<i>Gomphidius oregonensis</i>	25							
<i>Gomphidius smithii</i>	7.5		9.6	5.6		10	2.3	
<i>Gomphidius subroseus</i>	16	6.1	32	11	13	67	4.9	
<i>Gomphus clavatus</i>							32	
<i>Gomphus floccosus</i>		65			11	67		
<i>Hebeloma olympianum</i>	5.4						13	
<i>Hydnellum aurantium</i>				10				
<i>Hydnum repandum</i>	477			179	8.2		232	
<i>Hydnum umbilicatum</i>			3.6					
<i>Hygrophorus bakerensis</i>	8.3		2.7		14		23	
<i>Hygrophorus camarophyllus</i>	27		2.5				19	
<i>Hygrophorus eburneus</i>	19		16			19	11	
<i>Inocybe acuta</i> gp.			2.3		4			
<i>Inocybe castanea</i> gp.				1.6		1.6		0.3
<i>Inocybe fuscodisca</i> sensu Stuntz							2.8	
<i>Inocybe geophylla</i>						1.4		
<i>Inocybe geophylla</i> v. <i>lilacina</i> sensu Kuyper			1.4	21	4.3	0.9		1.1
<i>Inocybe hirsuta</i>						29		15
<i>Inocybe lanuginosa</i>				1.6		0.4		
<i>Inocybe nitidiuscula</i>				1.4				
<i>Inocybe obscura</i> complex						2.1		
<i>Inocybe ochroalba</i>				0.5		14		
<i>Inocybe olympiana</i>							37	
<i>Inocybe pudica</i>				2.4		6.6		
<i>Inocybe pusio</i> gp. sensu Kuyper				0.5	3.2		2.4	4.8
<i>Inocybe radiata</i> gp.				0.9				
<i>Inocybe sororia</i>								7.7
<i>Inocybe umbrina</i> gp.						2		4
<i>Inocybe xanthomelas</i>					11			0.7
<i>Laccaria amethysteo-occidentalis</i>	3		0.8	19		21		
<i>Laccaria bicolor</i>	2.8			1.8		0.6	36	47
<i>Laccaria laccata</i>	13					15		
<i>Lactarius cascadenensis</i>							3.6	
<i>Lactarius fallax</i>							35	25
<i>Lactarius kaufmanii</i>			76			14	93	
<i>Lactarius olivaceoumbrinus</i>								6.3
<i>Lactarius pallescens</i>						126	20	
<i>Lactarius pseudomicidus</i>	98		98	1.9	37	55	111	

Table 4. (concluded).

	Ga1	Ga2	Ga3	PsG1	BP1	BP2	BP3	Va1
<i>Lactarius rubrilactis</i>	14		23	147	26	52	1.4	
<i>Lactarius substriatus</i>			5.6	37	1.4	70	4.4	80
<i>Phellodon atratus</i>				2.6				
<i>Phellodon melaleucus</i>				8.1				
<i>Phellodon tomentosus</i>	6.1		49					
<i>Phylloporus rhodoxanthus</i>						2.8		
<i>Ramaria cf. longispora</i>							22	
<i>Rozites caperata</i>						24	42	
<i>Russula bicolor</i>	2.4			14		3.5	3.2	25
<i>Russula brevipes</i>				53	186			
<i>Russula cascadenis</i>			20					
<i>Russula crassotunicata</i>						15		
<i>Russula cremoricolor</i>								7
<i>Russula laurocerasi</i>						3.6		
<i>Russula montanus</i>				21				
<i>Russula occidentalis</i>						13		
<i>Russula pelargonica</i>	6.3		4.9	43	2.7	51		
<i>Russula queletii</i>	8.5		8.9		8.4	6.1	28	20
<i>Russula sp. 3</i>	66							
<i>Russula xerompelina</i>					8		10	
<i>Sarcodon fuscoindicus</i>				11				
<i>Suillus granulatus</i>	13							
<i>Suillus lakei</i>		5.4	2.8	28		321		
<i>Suillus punctatipes</i>			14					
<i>Tricholoma atroviolaceum</i>						18	63	
<i>Tricholoma aurantium</i>				6.2				
<i>Tricholoma flavobrunneum</i>	10							
<i>Tricholoma flavovirens</i>	26		25			21		
<i>Tricholoma focale</i>		14		16				
<i>Tricholoma odorum</i>					14			
<i>Tricholoma portentosum</i>						64		
<i>Tricholoma saponaceum</i>						5.1		19
<i>Tricholoma terriferum</i>			27					
<i>Tricholoma vaccinum</i>	4.9				11	5.3		
<i>Tricholoma virgatum</i> gp.						16		

dus (0.05 kg/ha) and *Suillus lakei* (0.05 kg/ha) (Table 4). Mean fall sporocarp standing crop at seven stands (Va1 omitted) was positively correlated with mean annual precipitation ($r^2 = 0.51$, $p < 0.07$) (Fig. 4, Table 3).

Mean EMF species richness was 41 per stand, and ranged from 19 to 62 species per stand (Fig. 5). Stand sample richness ranged from 0 to 39 species. Most species (147) occurred in fall; only 3 were found in spring. Individual species were often restricted to a single stand and year (Fig. 5). Combining all stands, 35% of species occurred in both years; an average of 5% of species occurred both years at any given stand. Richness at seven stands (Va1 omitted) was positively correlated ($r^2 = 0.66$, $p < 0.024$) with mean annual precipitation (Table 3, Fig. 6).

Eighty-four fungal taxa occurred at two or more stands and were included in the ordination. DCA axis 1 had an eigenvalue of 0.71 and was 5.75 standard deviations long (Fig. 7). This axis was negatively correlated with precipitation and cover by *Vaccinium* spp. and positively correlated

with cover by *Gaultheria shallon* and canopy cover by *Tsuga heterophylla* (Table 3).

Discussion

This study demonstrated that ectomycorrhizal macro-mycete fruiting patterns change in relation to environmental conditions even when dominant host species are constant. Species richness and sporocarp standing crop in the sample plots were correlated with mean annual precipitation. The stands included four vegetation types representing a wet to dry gradient. The wettest stand was Va1, which receives an estimated mean annual precipitation of 454 cm. It is probably transitional to the *Picea sitchensis* zone that occupies lower river terraces about 50 m from this stand. Stands at the dry extremes included Ga2 and PsG1. The former was less productive, possibly because of its higher elevation and shorter growing season; PsG1 is in the *Pseudotsuga menziesii* zone and includes such warm-dry stand indicator plant

Fig. 4. Regression plot of sporocarp standing crop versus mean annual precipitation.

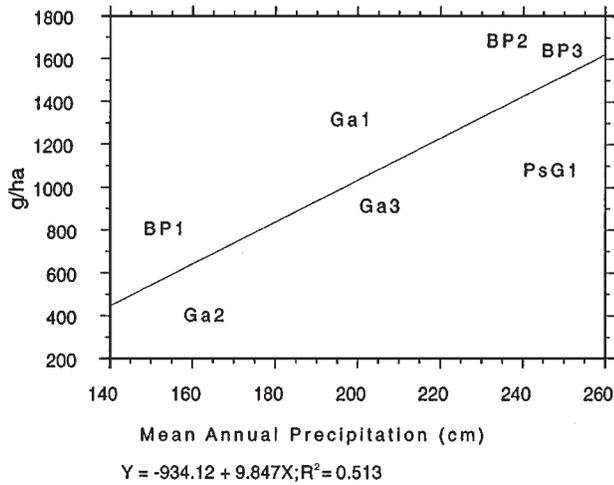
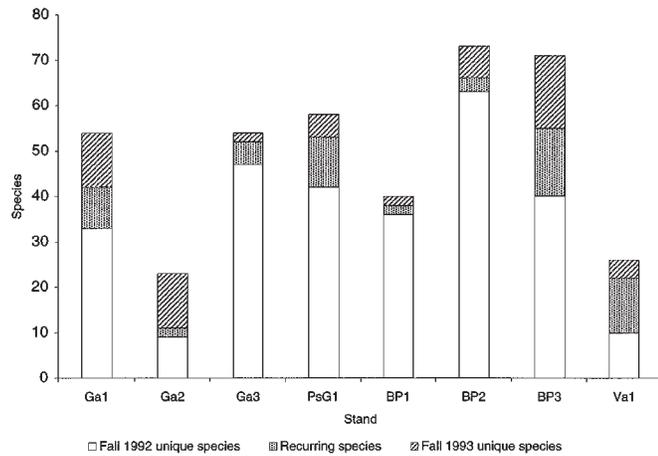


Fig. 5. Annual variation in EMF species occurrence during 1992 and 1993.



species as *Holodiscus discolor* and *Prunus emarginata* (Table 2; Leshner and Henderson 1992).

Our results illustrate the influence of moisture availability on fruiting of EMF. Sporocarp standing crop and EMF species richness increased linearly with average annual precipitation over the well-sampled portion of the precipitation gradient. Sporocarp standing crop and EMF species richness were correlated, possibly because of the increased probability of encountering productive species when more species are present (Tilman 1999). Both were sharply lower at the wettest stand (Va1, ca. 450 cm/year; Table 1) in comparison with the next driest stand (BP3, ca. 250 cm/year; Table 1). These data lead us to suspect that EMF species richness and sporocarp biomass have a unimodal or hump-shaped distribution with respect to precipitation. Rosenzweig and Abramsky (1993) and Guo and Berry (1998) hypothesize that hump-shaped distributions like this can serve as a model for the general response of species diversity to precipitation. Our data support this model; both fungal species richness and sporocarp standing crop reach their highest values in the middle of the precipitation gradient. The EMF species re-

Fig. 6. Regression plot of EMF species richness versus mean annual precipitation.

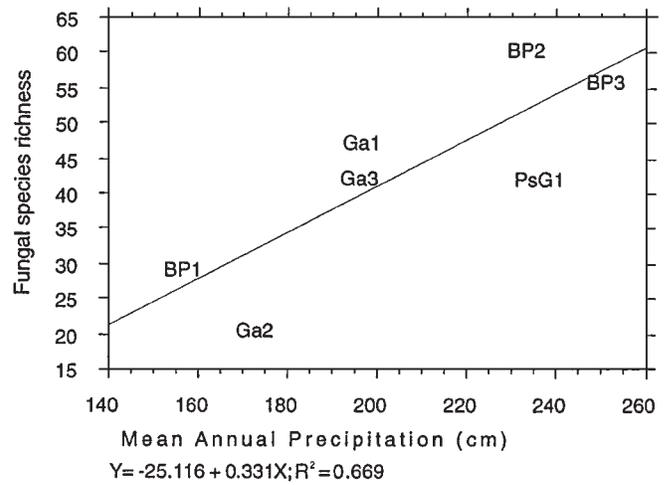
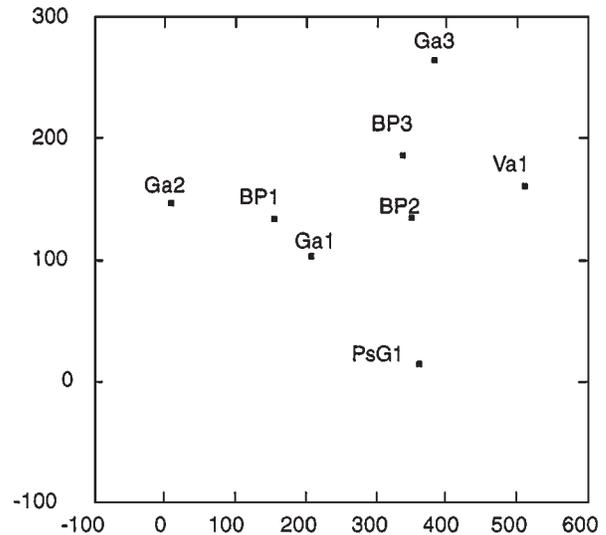


Fig. 7. Fungi species DCA stand scores on axes 1 and 2, with eigenvalues of 0.71 and 0.38, respectively.



stricted to either end of the precipitation gradient (but not to a single stand) included *Cortinarius olympianus* and *Russula brevipes* at the drier stands and *Amanita constricta* and *Boletus mirabilis* at the wetter ones.

Comparisons of species richness between different studies of EMF are hampered by differences in sampling methods. Most investigators have used contiguous quadrats, which are resampled several times over the course of a study. We sampled noncontiguous plots distributed along transects and we sampled a new transect at each sampling time, as did Luoma et al. (1991) and North et al. (1997). Therefore, even though our stand samples were modest in size, they were dispersed over a greater surface area than those from studies using adjacent and resampled plots. Higher richness may result from sampling a new transect at each sampling time or from the noncontiguous spacing of plots.

Our EMF species richness values were higher than those from similar studies in eastern North America that spanned

greater habitat diversity. Bills et al. (1986) sampled 3072 m² for 3 years in *Fagus*- and *Picea*-dominated forests. They found 54 EMF species, 27–35 species per forest type. Villeneuve et al. (1989) repeatedly sampled 8000 m² for 2 years in *Abies*-, *Betula*-, and *Picea*-dominated forests, finding 84 total EMF species (26–37 per forest type). In contrast, we found 150 EMF species in a single forest zone (total cumulative fall sample area = 10 400 m²), and up to 39 species in a single 400-m² stand sample. This higher richness in the area that we sampled could be due to greater EMF species richness associated with *Pseudotsuga menziesii* and *Tsuga heterophylla*, our sampling of late seral stands, or the use of a dispersed sampling design.

We found most species in a single stand and year. Only about 5% of the species occurred both years at a particular stand. Combining the data from all stands, 35% of species occurred both years. This annual variation may be explained by (i) dispersed sampling detecting species locally restricted in a stand; (ii) species fruiting in response to specific weather conditions; and (iii) the occurrence of annual species that are not persistent from year to year. The high annual variation in EMF species occurrence points out the need for long-term studies so that we can better understand their community structure and habitat preferences.

We found that the five most productive epigeous EMF species produced only 25% of total standing crop. By contrast, Luoma et al. (1991) found that five species of hypogeous fungi accounted for 73% of the total hypogeous standing crop, and North et al. (1997) found a single hypogeous species accounted for over 90% of the total hypogeous standing crop. For the epigeous fungi that we studied, summing the standing crop of the 43 most productive species was required to reach 75% of the total. This might indicate profound differences in resource partitioning by epigeous and hypogeous fungi.

Hypogeous sporocarps seem to fruit more abundantly and with less seasonal variation than epigeous sporocarps. Luoma et al. (1991) and North et al. (1997) found 50–60% of standing crop in spring for hypogeous sporocarps, and we found over 90% of standing crop in fall for epigeous sporocarps. The more uniform seasonal distribution of hypogeous sporocarp production compared with epigeous make hypogeous sporocarps a more reliable food supply. This may be one reason why rodent mycophagists tend to specialize on the hypogeous species (Maser et al. 1978).

If fungal species differ greatly among stands with similar vegetation, as seems to be the case, then conserving fungal diversity requires protection of more area than is required to conserve the higher plants. The high species richness of EMF also points to the need for intensive sampling to obtain data regarding EMF communities. Our finding of higher species richness than several studies in eastern North America spanning a greater diversity of host taxa supports Trappe and Fogel's (1977) contention that *Pseudotsuga menziesii* hosts an exceptional diversity of mycorrhizal fungi.

The fungal species richness and community structure reported here represent only the most conspicuous and accessible part of a larger community. More species would have been found if we had sampled hypogeous sporocarps or ectomycorrhizal root tips (Luoma et al. 1991; Gardes and

Bruns 1996). Furthermore, abundance of sporocarps does not necessarily reflect abundance of mycorrhizae (Gardes and Bruns 1996; Gehring et al. 1998). Hypogeous sporocarps and ectomycorrhizae will be included in a future study.

Despite the well-known relation between weather and sporocarp production (i.e., mushrooms are produced following rain (Eveling et al. 1990)), climate rarely has been studied as a cause of fungal species distributions. Studies of fungal ecology focus on host and substrate influences, which mycologists have long considered as primary factors determining species distributions (Grainger 1946; Kost 1992; Tyler 1992). Our data suggest that fungal species respond to climate on a regional scale.

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References

- Abacus Concepts. 1992. Abacus concepts, Statview. Abacus Concepts Inc., Berkeley, Calif.
- Arnolds, E. 1988. The changing macromycete flora in the Netherlands. *Trans. Br. Mycol. Soc.* **90**: 391–406.
- Arnolds, E., and deVries, B. 1993. Conservation of fungi in Europe. *In Fungi of Europe: investigation, recording and conservation. Edited by D.N. Pegler, L. Boddy, B. Ing, and P.M. Kirk.* Royal Botanic Gardens, Kew. pp. 211–230.
- Barbour, M.G., Burk, J.H., and Pitts, W.D. 1987. *Terrestrial plant ecology*, 2nd ed. Benjamin/Cummings Pub. Co., Menlo Park, Calif.
- Bills, G.F., Holtzmann, G.I., and Miller, O.K., Jr. 1986. Comparison of ectomycorrhizal basidiomycete communities in red spruce versus northern hardwood forests of West Virginia. *Can. J. Bot.* **64**: 760–768.
- Buckingham, N.M., Schreiner, E.G., Kaye, T.N., Burger, J.E., and Tisch, E.L. 1995. *Flora of the Olympic Peninsula*. Northwest Interpretive Association, Seattle, Wash.
- Cooke, W.B. 1955. Fungi, lichens and mosses in relation to vascular plant communities in eastern Washington and adjacent Idaho. *Ecol. Monogr.* **25**: 119–180.
- Eveling, D.W., Wilson, R.W., Gillespie, E.S., and Baitille, E. 1990. Environmental effects on sporocarp counts over fourteen years in a forest area. *Mycol. Res.* **94**: 998–1002.
- Fogel, R., and Hunt, G.A. 1979. Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. *Can. J. For. Res.* **9**: 245–256.
- Franklin, J.F., and Dyrness, C.T. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oreg.
- Gardes, M., and Bruns, T.D. 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* stand: above- and below-ground views. *Can. J. Bot.* **74**: 1572–1583.

- Gehring, C.A., Theimer, T.C., Whitham, T.G., and Keim, P. 1998. Ectomycorrhizal fungal community structure of pinyon pines growing in two environmental extremes. *Ecology*, **79**: 1562–1572.
- Guo, Q., and Berry, W.L. 1998. Species richness and biomass: dissection of the hump-shaped relationships. *Ecology*, **79**: 2555–2559.
- Grainger, J. 1946. Ecology of the larger fungi. *Trans. Br. Mycol. Soc.* **29**: 52–63.
- Hayes, J.P., Cross, S.P., and McIntire, P.W. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. *Northwest Sci.* **60**: 250–257.
- Henderson, J.A., Peter, D.H., Leshner, R.D., and Shaw, D.C. 1989. Forested plant associations of the Olympic National Forest. U.S. Dep. Agric. For. Serv. PNW Region R6 ECOL Tech. Pap. No. 001–88.
- Hill, M.O., and Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegatatio*, **42**: 47–58.
- Hitchcock, C.L., and Cronquist, A. 1976. *Flora of the Pacific Northwest: an illustrated manual*. University of Washington Press, Seattle, Wash.
- Hunt, G.A., and Trappe, J.M. 1987. Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand. *Can. J. Bot.* **65**: 438–445.
- Klironomos, J.N., and Kendrick, W.B. 1993. Research on mycorrhizas: trends in the past 40 years as expressed in the 'MYCOLIT' database. *New Phytol.* **125**: 595–600.
- Kost, G. 1992. Macrofungi on soil in coniferous forests. *In Fungi in vegetation science*. Edited by W. Winterhoff. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 79–111.
- Leshner, R.D., and Henderson, J.A. 1992. Indicator species of forested plant associations on National Forests of Northwestern Washington. U.S. Dep. Agric. For. Serv. PNW Region, R6-MBS-TP-041–1992.
- Luoma, D.L. 1989. Biomass and community structure of sporocarps formed by hypogeous ectomycorrhizal fungi within selected forest habitats of the H.J. Andrews Experimental Forest, Oregon. Ph.D. thesis, Oregon State University, Corvallis, Ore.
- Luoma, D.L., Frenkel, R., and Trappe, J.M. 1991. Fruiting of hypogeous fungi in Oregon Douglas-fir forests: seasonal and habitat variation. *Mycologia*, **83**: 335–353.
- Maser, C.M., and Trappe, J.M. 1984. The seen and unseen world of the fallen tree. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-164.
- Maser, C.M., Trappe, J.M., and Nussbaum, R.A. 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology*, **59**: 799–809.
- Massicotte, H.B., Molina, R., Luoma, D.L., and Smith, J.E. 1994. Biology of the ectomycorrhizal genus *Rhizopogon*. II. Patterns of host–fungus specificity following spore inoculation of diverse hosts grown in mono- and dual-cultures. *New Phytol.* **126**: 677–690.
- McCune, B., and Mefford, M.J. 1995. *PCORD*. Multivariate analysis of ecological data. Version 2.0. MJM Software Design, Gleneden Beach, Ore.
- Miller, O.K., Jr. 1983. Ectomycorrhizae in the Agaricales and Gasteromycetes. *Can. J. Bot.* **61**: 909–916.
- Molina, R., and Trappe, J.M. 1982. Patterns of ectomycorrhizal host specificity and potential among Pacific Northwest conifers and fungi. *For. Sci.* **28**: 423–458.
- Molina, R., Massicotte, H.B., and Trappe, J.M. 1992. Specificity phenomena in mycorrhizal symbiosis: community-ecological consequences and practical implications. *In Mycorrhizal functioning: an integrative plant–fungal process*. Edited by M.F. Allen. Chapman & Hall, London, U.K. pp. 357–423.
- Nantel, P., and Neuman, P. 1992. Ecology of ectomycorrhizal basidiomycete communities on a local vegetation gradient. *Ecology*, **73**: 99–117.
- National Oceanic and Atmospheric Administration. 1978. *Climate of Washington. Climatography of the United States No. 60*. National Oceanic and Atmospheric Administration, Washington D.C.
- North, M., Trappe, J., and Franklin, J. 1997. Standing crop and animal consumption of sporocarps in Pacific Northwest forests. *Ecology*, **78**: 1543–1554.
- Norton, J.M., Smith, J.L., and Firestone, M.K. 1990. Carbon flow in the rhizosphere of ponderosa pine seedlings. *Soil Biol. Biochem.* **22**: 449–455.
- O'Dell, T.E., Smith, J.E., Castellano, M.A., and Luoma, D.L. 1996. Diversity and conservation of forest fungi. *In Managing forest ecosystems to conserve fungus diversity and sustain wild mushroom harvests*. Edited by R. Molina and D. Pilz. U.S. Dep. Agric. Gen. Tech. Rep. PNW-GTR-371. pp. 5–18.
- Perry, D.A., Amaranthus, M.P., Borchers, J.G., Borchers, S.L., and Brainerd, R.E. 1989. Bootstrapping in ecosystems. *Bioscience*, **39**: 230–237.
- Perry, D.A., Margolis, H., Choquette, C., Molina, R., and Trappe, J.M. 1992. Ectomycorrhizal mediation of competition between coniferous tree species. *New Phytol.* **112**: 501–511.
- Phillips, E.L., and Donaldson, W.R. 1972. *Washington climate for these counties: Clallam, Grays Harbor, Jefferson, Pacific and Wahkiakum*. Cooperative Extension Service Publication EM 3708. Washington State University, Pullman, Wash.
- Rosenzweig, M.L., and Abramsky, Z. 1993. How are diversity and productivity related? *In Species diversity in ecological communities*. Edited by R.E. Ricklefs and D. Schuller. University of Chicago Press, Chicago, Ill. pp. 52–65.
- Simard, S.W., Jones, M.D., Durall, D.M., Perry, D.A., Myrold, D.D., and Molina, R. 1997a. Reciprocal transfer of carbon isotopes between ectomycorrhizal *Betula papyrifera* and *Pseudotsuga menziesii*. *New Phytol.* **137**: 529–542.
- Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M., and Molina, R. 1997b. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature (London)*, **388**: 579–582.
- Smith S.E., and Read, D.A. 1997. *Mycorrhizal symbiosis*. 2nd ed. Academic Press, London.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**: 1455–1474.
- Trappe, J.M., and Fogel, R.D. 1977. Ecosystematic functions of mycorrhizae. *Colo. State Univ. Range Sci. Dep. Range Sci. Ser.* **26**: 205–214.
- Tyler, G. 1992. Tree species affinity of decomposer and ectomycorrhizal macrofungi in beech (*Fagus sylvatica* L.) oak (*Quercus robur* L.) and hornbeam (*Carpinus betulus* L.) forests. *For. Ecol. Manage.* **47**: 269–284.
- USDA and USDI. 1994a. Final supplement environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. U.S. Dep. Agric. For. Serv.; U.S. Dep. Interior, Bureau of Land Management. 2 vol.
- USDA and USDI. 1994b. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl (plus Attachment A: standards and guidelines). U.S. Dep. Agric. For. Serv.; U.S. Dep. Interior, Bureau of Land Management.

- Villeneuve, N., Grandner, M.M., and Fortín, J.A. 1989. Frequency and diversity of ectomycorrhizal and saprophytic macrofungi in the Laurentide Mountains of Quebec. *Can. J. Bot.* **67**: 2616–2629.
- Whittaker, R.H., and Niering, W.A. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. *Ecology*, **56**: 771–790.
- Winterhoff, W. (*Editor*). 1992. *Fungi in vegetation science*. Kluwer Academic Publishers, The Netherlands.
- Zobel, D.B., McKee, A., Hawk, G.M., and Dyrness, C.T. 1976. Relationships of environment to composition, structure and diversity of forest communities of the central western Cascades of Oregon. *Ecol. Monogr.* **46**: 135–156.